Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators

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Abstract: Ship rats (*Rattus rattus*) were removed from sites on Pearl Island, southern Stewart Island, in 2004 and 2005, to test whether they excluded Pacific rats (*R. exulans*) or Norway rats (*R. norvegicus*) or both from podocarp-broadleaf forest. As predators can influence habitat use in rodents, Pearl Island was selected because no mammalian predators of rodents are present. Rats were trapped in two other habitats to clarify rat distribution on the island and to obtain samples for stable isotope investigation of food partitioning within habitats. The experimental removal of ship rats failed, as Pacific rats were found to share forest and shrubland with ship rats. This result contrasted with the restricted distribution of Pacific rats on Stewart Island. Ship rats were ubiquitous, and appear to have been the dominant species in podocarp-broadleaf forest on Pearl Island. The largest species, the Norway rat, was trapped only on the foreshore of Pearl Island, but on Stewart Island it is more widespread. Ship rats and Norway rats were partitioning the coastal habitat by exploiting different food sources. Stable isotopic ratios ($\delta^{15}N$ and $\delta^{13}C$) in muscle samples from Norway rats revealed a strong marine signature, suggesting intensive foraging in the intertidal zone. Ship rats trapped in the same habitat exhibited mixed terrestrial and marine sources in their diet. There was little obvious partitioning between ship rats and Pacific rats in forest, except a possible delay in breeding in Pacific rats relative to ship rats. Whether Norway rats select the intertidal zone to forage, or were excluded from forest by ship rats is unknown, but competitive exclusion is likely. Estimated densities of rats were low (2.1–5.1 rats ha^{-1} in forest, 1.42 rats ha^{-1} in shrubland) and similar to other New Zealand sites with low soil fertility. Further research will be required to elucidate the roles of food quality, habitat structure and predation in facilitating habitat selection in these species.

Keywords: *Rattus* spp; resource partitioning; stable isotopes; habitat use; ship rat; Norway rat; Pacific rat; Stewart Island; predators; competition

Introduction

Sympatric rodent species partition resources such as food or space (Grant, 1972). The degree to which a species can partition resources depends on the species' ability to use and defend a resource, and its vulnerability to predation, relative to other competing species within a habitat (Morris *et al.*, 2000). Ship rats (*Rattus rattus*) are generally regarded as the superior competitor of the three rat species now resident in New Zealand (Russell and Clout, 2004). Taylor (1978) suggested that this may explain why the distributions of the larger Norway rat (*R. norvegicus*) and the smaller Pacific rat (*R. exulans*) are restricted in comparison to that of the ship rat. It is thought that interference competition is probably the principal mechanism for partitioning of habitat by the three rat species (Yom–Tov *et al.*, 1999; Russell and Clout, 2004), although predation may play a role (Taylor, 1978). Predation and competition may also interact to alter the apparent competition between rodent species

in different habitats (Norrdahl and Korpimaki, 1993; Morris, 1996).

Predation by cats (*Felis catus*) is not thought to determine the distribution of Norway rats (Childs, 1986; Fitzgerald *et al.*, 1991). It has been suggested that non-commensal Norway rats in New Zealand are restricted to sites near water by predation by mustelids, particularly stoats (*Mustela erminea*) (Taylor, 1978), but data from islands lacking mustelids suggest that interference competition with ship rats restricts the distribution of Norway rats (Harper *et al.*, 2005).

The distribution of Pacific rats appears to be affected by predation or interference competition from larger rodents, or both (Atkinson and Towns, 2005). Modelling of the distribution of rats and circumstantial evidence led Russell and Clout (2004) to conclude that "the absence of Pacific rats on islands is currently most strongly influenced by the presence of ship rats". Pacific rats do, however, share habitats with ship rats; on Stewart Island with Norway rats present (Sturmer,

1988; Harper *et al.*, 2005); in the south-west of the South Island, often with mice present (King and Moller, 1997; Ruscoe, 2004); on both Great Barrier Island (Atkinson, 1978) and New Caledonia (Rouys and Theuerkauf, 2003) without Norway rats but with mice present. These distribution overlaps imply mechanisms other than interference competition are necessary to explain the perceived exclusive occupation of islands by Pacific rats and ship rats.

Stewart Island, in southern New Zealand, is an ideal setting for an investigation of whether predation and interference competition cause niche partitioning in rats because three species are present on the main island and a few nearby islands, such as Pearl Island (Grant, 1986). Mice are not present. Podocarp-broadleaf forest on Stewart Island is dominated by ship rats, with low numbers of Norway rats present (Hickson *et al.*, 1986; Sturmer, 1988; Harper *et al.*, 2005). Pacific rats are rarely trapped in this forest type (Sturmer, 1988; Harper *et al.*, 2005). In dry sites with a structurally simple forest, low canopy height and ample ground cover, Pacific rats predominate (Sturmer, 1988; Harper *et al.*, 2005). Norway rats are the most common rat in subalpine shrubland (Harper *et al.*, 2005). They are found next to streams and in coastal forest on Stewart Island (Hickson *et al.*, 1986; Sturmer, 1988). Feral cats are present on Stewart Island and prey primarily on rodents (Karl and Best, 1982; Harper, 2005b). The population density of cats on Stewart Island is very low (Harper, in press), however, and the feral cat population is strongly limited by rat abundance (Harper, 2005b). There are no mustelids (*Mustela* spp.) present. On some smaller satellite islands, including Pearl Island, there are no mammalian predators, other than the rats themselves.

The arrival dates of the three rats species present on Pearl Island are unknown, but are probably similar to their arrival dates on Stewart Island. Pacific rats were probably introduced about 1400–1500AD (Holdaway, 1999). They had been established for maybe 400 years before Norway rats were introduced by the first Europeans about 1790–1800 (Atkinson, 1973). Norway rats became very common on Stewart Island by the late 1800s (Thompson, 1922). Ship rats were introduced to Stewart Island about 1890 (Atkinson, 1973). As each of the European rat species became established, it appears to have largely excluded the incumbent species from the newcomer's favoured habitats (Harper *et al.*, 2005).

The role of competition can be tested experimentally by selectively removing one or more species across a habitat boundary (Higgs and Fox, 1993). Moller (1977) suggested testing the hypothesis that the larger species restrict Pacific rats to areas of dense ground cover, by selective removal of a larger congener from forest on a grassland/forest boundary. On Stewart Island, therefore, the selective trapping of ship rats in a grid

across a forest/shrubland boundary may result in Pacific rats occupying the niche space left vacant in the forest (Harper *et al.*, 2005). The absence of a compounding variable, predation by other mammalian predators, would clarify the role of interference competition in the habitat use of the three rat species.

Schoener's (1974) analysis of studies of resource apportioning showed that niches are partitioned most often by habitat, then by food. Stable isotopic analysis is now a well-established tool in assessing food resource partitioning in a variety of animal guilds (e.g., Herrera *et al.*, 2003; Mauffrey and Catzellis, 2003; Stewart *et al.*, 2003; Baugh *et al.*, 2004). Stable isotopic analysis has the advantage over gut or faecal studies of providing an integrated signal of gross dietary composition over defined periods of an animal's life. The quantification of the source of assimilated, rather than just ingested food items, is also possible with this technique, so stable isotopic analysis (using carbon and nitrogen isotope ratios) was used to investigate partitioning of food resources by rat species on Pearl Island.
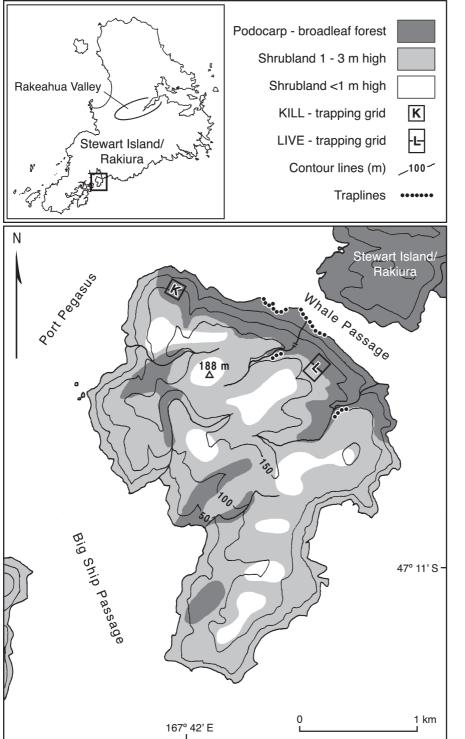
Methods

Study Site

The study area was on 500-ha Pearl Island (47° 11'S, 167° 42'E), which bounds part of the north-east portion of Port Pegasus, Stewart Island (Fig. 1). The island is a shrubland-covered plateau at about 120–180 m a.s.l., with a very steep coast on all sides. The climate is cool and very windy, with an annual rainfall estimated at 2000 mm, falling over 230 rain-days (Sansom, 1984). At Southwest Cape, about 20 km south-west of Pearl Island, the annual average temperature is 10.3 °C. Soils on Stewart Island are generally acidic and of very low fertility (Wilson, 1987). The soil fertility on Pearl Island should be poorer than on many other islands around Stewart Island, as it has almost no nesting seabirds.

On the northern coast, facing Whale Passage and the North Arm of Port Pegasus (Fig. 1), there is a narrow strip of coastal forest consisting of muttonbird scrub (*Senecio reinoldii*), *Hebe elliptica*, southern rata (*Metrosideros umbellata*), broadleaf (*Griselinea littoralis*), inaka (*Dracophyllum longifolium*), with many groves of tree ferns (*Dicksonia squarrosa*) and supplejack (*Ripogonum scandens*).

On well-drained slopes in northern and sheltered sites, from near sea-level to about 120 m a.s.l., there is a podocarp-broadleaf forest of emergent rimu (*Dacrydium cupressinum*) over a canopy of kamahi (*Weinmannia racemosa*), southern rata, miro (*Prumnopitys ferruginea*), and some Hall's totara (*Podocarpus hallii*). The understorey included young canopy trees, shrubs and tree-ferns. Crown fern (*Blechnum discolor*) dominated the ground cover.

Figure 1. Location and habitat map of Pearl Island, showing the location of the trapping grids and trap-lines.

On the plateau and southern coast, low (1–3 m) shrubland is dominated by manuka (*Leptospermum scoparium*), yellow-silver pine (*Lepidothamnus intermedius*), pink pine (*Halocarpus biformis*) and inaka. Ground cover included tussock sedge (*Gahnia procera*), many small herbs and some areas of wire rush (*Empodisma minus*), coral lichen (*Cladia retipora*), *Lycopodium* species, or tangle fern (*Gleichenia dicarpa*). In very exposed sites the shrubs were very stunted (< 1 m high).

Weka (*Gallirallus australis*), a large (~800 g) endemic rail, were the only potential predator of rats on the island, apart from other rats, but they were in low numbers (pers. obs.). Weka are opportunistic omnivores, taking mainly invertebrates and fruit (Marchant and Higgins 1993), although they can kill ship rats (Brothers and Skira, 1984). There were no cats or possums (*Trichosurus vulpecula*). Deer, probably white-tailed (*Odocoileus virginianus borealis*), occasionally swim from Stewart Island, but there was no permanent population.

Habitat partitioning, density and breeding by rats

Two rat-trapping grids were established on Pearl Island in late March 2004, 1200 m apart in podocarp-broadleaf forest on the steep northern slope (Fig. 1) and ship rats were removed from the grids to see if other rat species moved into the vacant sites. The grid patterns ran nearly north-east to south-west and perpendicular to the slope. A compass and measuring tape were used to establish the trap positions on the grids. The four corners of each grid were located by a Garmin GPS to within 10 m accuracy. The first grid (kill-grid: K) consisted of 49 "Victor" snap-traps, baited with a mixture of rolled oats and peanut butter. The traps were under 12 mm mesh covers, in a grid pattern of 7 × 7 traps, at 20-m intervals, and traps and covers were secured with wire stakes. The total area of the grid was 120 m by 120 m (1.4 ha). The traps were left unset for three days before trapping began on 31 March 2004 and trapping continued for seven days.

The other grid (live-grid: L) was established across an obvious vegetation boundary, between podocarp-broadleaf forest on the steep northern slope, and subalpine shrubland on the adjacent plateau. Grid L consisted of 50 small-mammal cage-traps, set in a grid pattern of 10 × 5 traps at 25-m intervals. The cage-traps were baited with a mixture of rolled oats and peanut butter smeared on diced carrot. Rats caught in live-traps sometimes die of hypothermia (Hickson *et al.*, 1986), so the cage-traps had plastic covers attached to their roofs so rats would not get wet during overnight rain. Generous amounts of bait were left as a food source. The total area of the grid was 200 m × 100 m (2 ha), bisected by the vegetation boundary (Fig. 1).

The location of the vegetation boundary was recorded by GPS. The grid was operated for 12 days from 26 March 2004.

Traps were checked every morning and all rats removed. Rats in podocarp-broadleaf forest on Grid L were killed with an overdose of Halothane®. Rats caught in the shrubland on Grid L were anesthetised with Halothane®, identified to species, sexed, weighed, and ear-tagged for individual identification and then released. Dead rats were processed on the day of capture, following the protocol of Cunningham and Moors (1996), and weight (g), head-body length (HBL) and tail length (TL) (mm), species, sex, and approximate age (adult or juvenile, determined by the presence of a perforate or imperforate vagina for females and presence of absence of visible tubules within the cauda epididymis for males) were recorded. The numbers of embryos or uterine scars were recorded for adult females. Muscle samples for stable isotopic analysis were taken from the back left leg of each rat. Any scavenged rats were identified to species, sex, and age so far as possible, depending on the state of the remains.

The 'Zippin removal' technique (Zippin, 1958) was used to estimate the density of rats caught on the trapping grids. Each night's catch was plotted against the cumulative total to estimate the number of rats left on the trapping-grid (Brown *et al.*, 1996).

To estimate the effective trapping area (ETA) for ship rats, a boundary strip was added to the edge of the trapping grids (Dice, 1938). The width of the boundary strip was set by adding the radius (71 m) of a circular average home range (0.54 ha) of ship rats from Stewart Island (Hickson *et al.*, 1986). To establish the ETA for Pacific rats, the radius of circular average home range of an adult female Pacific rat trapped on the shrubland grid was used. The distances between consecutive capture sites were measured to derive a range length and width to estimate home range size.

Trap-lines for Norway rats were established next to two streams on either side of Grid L on Pearl Island in early April 2004, and along the northern coast in June 2005 (Fig. 1). The streams were in deep northeast-facing gullies that received no direct sunlight in April, so they were cold and damp. The stream trap-lines consisted of five live-traps, 25 m apart, set for four nights, and baited with a mixture of peanut butter and rolled oats. All trapped rats were killed by an overdose of Halothane®. The coastal trap-lines consisted of two lines of 25 'Victor' snap-traps each, placed at c. 25-m intervals at, or near, the high-tide line. The two lines were separated by c. 150 m because access to the coast was difficult. The traps were set for two consecutive nights over 15–17 June 2005, and baited with a mixture of rolled oats and peanut butter. The shoreline was generally rocky, with steep to vertical slopes to the forest. It was partially exposed to surf entering Whale Passage from the open sea.

The rate of rat capture was defined as the number of rats (R) caught per 100 trap nights (TN), and given as R/100TN. Capture rates on the two lines were averaged to obtain a mean capture rate, and binomial confidence intervals were derived from these.

Stewart Island reference comparisons

Muscle samples were obtained from ship rats trapped in podocarp-broadleaf forest on Stewart Island. These samples provided comparative data for ship rats from forest at least 2 km from the sea. Rats were trapped in the Rakeahua Valley in June 2005 (Fig. 1), using the methods and trap-lines described in Harper (2005a).

Food partitioning using isotopic analysis

Muscle tissue samples were stored frozen in a gas-powered freezer in the field, and kept frozen on return to the mainland. Four sub-samples from each of the five groups; Pearl Island Norway rats, Pearl Island coastal ship rats, Pearl Island forest ship rats, Pearl Island Pacific rats, and forest ship rats from Stewart Island, were analysed.

Isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) were measured by Iso-Trace New Zealand Ltd, Dunedin, using isotope ratio mass spectrometry (IRMS; Hydra® 20/20 mass spectrometer). Stable isotopes are expressed in δ notation (in parts per thousand; per mil; ‰) as follows:

$$\delta X(‰) = 1000 \times (R_{sample} - R_{standard}) / R_{standard}$$

where X is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C and R is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$ as measured for the samples and relevant standards (atmospheric N_2, V D P B, respectively). The notations ($\delta^{13}C$ and $\delta^{15}N$) refer to the enrichment (positive values) or depletion (negative values) relative to these standards. Turnover time for muscle tissue is c. 4 weeks (Dalerum and Angerbjörn, 2005), so the ratios reflect the diet during the period before death.

All the dietary values were corrected for fractionation from diet to muscle, using values of +0.5‰ for $\delta^{13}C$ for gerbils *Meriones unguienlatus* (Tieszen *et al*., 1983) and +3.0‰ for $\delta^{15}N$, as a mean value derived from values for harp seal *Pagophilus groenlandicus* and red fox *Vulpes vulpes* (Kelly, 2000). Literature data were used in absence of information for most marine species in New Zealand (Hobson *et al*., 1994; Beavan and Sparks, 1998; Hobson *et al*., 1999). The rat isotopic signatures are plotted with data from inshore marine species and possible dietary items from the forest food web for comparative purposes. These marine species included blue penguin *Eudyptes minor*, intertidal amphipods (D. Hawke, Christchurch Polytechnic Institute of Technology, Christchurch, unpublished data), a crab *Hemigrapsus* sp., Californian

mussel *Mytilis californianus,* and an intertidal fish species *Xiphister atropurpureus*. The forest species included a beetle (Carabidae) and weta *Hemiandrus* sp., from Kapiti Island (Beavan and Sparks, 1998), a millipede *Harpaphe* sp. (Hobson *et al*., 1999), a terrestrial amphipod (Talitridae) and nikau palm *Rhopalostylis sapida* fruit (Hawke and Holdaway, 2005), trees, kahikatea *Dacrycarpus dacrydioides* (Hicks and Labroyrie, 1999) and rata leaves.

Results

Habitat use

The experimental removal of selected species within the L grid failed as Pacific rats were found sharing the forest with ship rats. No Norway rats were trapped in forest. On Grid K, three Pacific rats (21%) and 11 ship rats (79%) were trapped over 343 trap-nights (Table 1). All three Pacific rats were adult males and seven (four females) of the ship rats (64%) were adults. Of the four females, three had placental scars, and none was pregnant.

On Grid L, in the podocarp-broadleaf forest, 22 rats were caught in 225 TN over nine days (Table 1). Eleven (50%) were Pacific rats and the rest were ship rats. The last three nights of trapping were ignored in the analysis because weka began to interfere with the traps to the extent that almost all traps were set off over this period. Five (45%) of the Pacific rats were adults. Both the adult females had placental scars and one was also pregnant. Two of the five adult ship rats were females. One female had 10 placental scars and the other escaped before she could be anesthetised. All live-trapped rats were alive and energetic at the morning trap check.

In the shrubland half of Grid L, only four rats were caught over 225 TN, including three Pacific rats (2 adults, 1 juvenile) and one adult male ship rat. Significantly fewer rats were caught in the shrubland half of the grid than in the adjacent podocarp-broadleaf forest (G-test for homogeneity, $G_{(adj.) (d.f. = 1)} = 535.9$, $P < 0.001$). One pregnant female Pacific rat was re-captured twice, once in the shrubland the next day, and again on the edge of the podocarp-broadleaf portion of the grid five days later. The one ship rat was re-captured twice, once in a trap 25 m away from the first trap site, and then again at the original trap-site. Both rats were killed by an overdose of Halothane® after their final capture.

Density of rats

The number of rats declined quickly over the trapping periods on both grids in podocarp-broadleaf forest and, in each instance, only one rat was trapped on each grid

Table 1. Numbers and age of three rat species trapped on trapping grids and trap-lines on Pearl Island, March–April 2004 and June 2005 and the Rakeahua Valley, June 2005. Binomial confidence in intervals are in parentheses.

| | Pacific rat | | Ship rat | | Norway rat | | Trap nights | Total rats trapped | Rats/ 100TN |
	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.			
Kill-grid (podocarp forest)	3	-	7	4	-	-	343	14	4.1 (2.3–6.8)
Live-grid (podocarp forest)	5	6	5	6	-	-	225	22	9.8 (6.2–14.4)
Live-grid (shrubland)	2	1	1	-	-	-	225	4	1.8 (0.5–4.5)
Stream trap-lines (podocarp forest)	1	-	1	4	-	-	40	5	12.5 (4.2–26.8)
Coastal trap-lines (high-tide line)	-	-	2	13	9	4	100	28	28.0 (19.5–37.8)
Total rats caught (Pearl Island)	**11**	**7**	**16**	**27**	**9**	**4**	**933**	**73**	**7.8 (6.2–9.7)**
Rakeahua trap-lines (podocarp forest)	-	-	5	6	-	-	100	11	11.0 (5.6–18.8)

by the fifth night. On Grid K, 14 rats had been caught by day five, but none on the last two nights of trapping. A simple regression of capture against cumulative total gave an estimated number of rats on the trapping area of the kill-grid of 14.4 (95% C. I. 13.2–16.9, Fig. 2). The estimated effective trapping area for the 11 ship rats was 8.45 ha⁻¹, which gave an estimated density of 1.3–1.38 ship rats ha⁻¹. The boundary strip for the estimated effective trapping area for Pacific rats was derived using the three captures of the adult female Pacific rat from the shrubland trapping grid. Her home range was estimated at 0.44 ha, which gave a home range radius of 33 m. Therefore the effective trapping area for Pacific rats was probably 3.8 ha, and the population density was calculated to be 0.79–0.84 Pacific rats ha⁻¹. The combined density for both species of rats was 2.09–2.22 rats ha⁻¹.

In the forested portion (100 × 100 m) of Grid L, 19 rats were caught in the first five days (nine ship rats, ten Pacific rats), by which stage the number of captures per night had declined to one. The regression of capture against the cumulative total gave an estimated 21 rats on the grid (95% C. I. 18.4 – 29.8, Fig. 2). For the estimated effective trapping area for ship rats of 7.44 ha, this would represent 1.21–1.38 ship rats ha⁻¹. Setting the estimated effective trapping area for Pacific rats at 3.1 ha, using the method described for the Grid K, yielded a minimum density of 3.22–3.68 Pacific rats ha⁻¹. The combined density for both species of rats was 4.43–5.06 rats ha⁻¹.

In the 100 × 100 m shrubland section of Grid L, only one ship rat and three Pacific rats were caught. No regression could be calculated for these captures, so the density was estimated from the total number of rats trapped. With effective trapping areas the same as for the forested section these yielded densities of 0.13 ha⁻¹ (1 rat in 7.44 ha) for ship rats, and 1.29 rats ha⁻¹ for Pacific rats (Total; 1.42 rats ha⁻¹). This density was about one-third (32%) of the density of rats in the forested portion of Grid L.
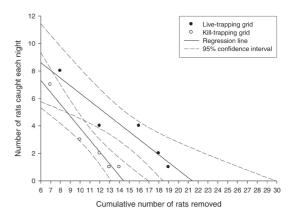

Figure 2. Nightly catch of rats plotted against the cumulative number of rats removed on two trapping grids in podocarp-broadleaf forest. Pearl Island, March–April 2004.

No Norway rats were caught in the two trap-lines next to the two streams over the combined total of 40 TN (Table 1). Five ship rats (one adult male; four juveniles) and one pregnant adult female Pacific rat were caught. In contrast, thirteen Norway rats (nine adults; four juveniles) were caught on the two coastal trap-lines over a combined 100 TN (Table 1). In addition, 15 ship rats (two adults; 13 juveniles) but no Pacific rats were trapped at the coast.

The relative abundance of rats caught on all sites is shown in Table 1. Only on the coast, where 28 rats were caught per 100 TN, was relative abundance > 13 rats per 100 TN. The table also shows the preponderance of ship rat (43) captures across all sites, with Pacific rats (19) about half this, and only 13 Norway rats.

Stewart Island reference comparisons

Eleven ship rats (4 adult females; 1 adult male; 5 juvenile males; 1 juvenile female) were caught on two trap-lines in the Rakeahua Valley over 100 TN. No other rat species were trapped. The three heaviest of the adult females had placental scars and one was lactating.

Breeding

It appears that ship rats had bred over late summer and early autumn 2004. Only adult female rats with placental scars and juvenile ship rats were trapped on both grids and on the stream trap-lines. Three pregnant Pacific rats and eight juveniles were caught during the same period. Analysis of data for the five adult female ship rats (excluding the adult female ship rat that escaped) and four Pacific rats, revealed a significant difference in the rate of pregnancy between the two species (two-sided Fisher's exact test, $P = 0.048$,) at the time of trapping.

Of the eight adult female Norway rats caught on the coastal trap-lines in June 2005, three (38%) had placental scars and none was pregnant. Both the adult female ship rats had placental scars and were not pregnant. Breeding had probably finished, as no pregnant rats were caught and the juveniles were relatively large. Seven of eight juvenile male ship rats weighed > 128 g, with a mean (± 1 s.e) weight of $153 ± 13.0$ g [mean adult male ($n = 7$) weight = $187.3 ± 11.4$ g], and the three juvenile male Norway rats were heavier than 143 g, with a mean weight of $164 ± 10$ g.

Isotopic analysis of food partitioning

$\delta^{13}C$ and $\delta^{15}N$ values were obtained from 20 rat muscle samples (Appendix 1). Sample precision was ± 0.3‰ for $\delta^{15}N$ and ± 0.03‰ for $\delta^{13}C$. The $\delta^{13}C$ and $\delta^{15}N$ values differed significantly between the five sample groups (Kruskal-Wallis non-parametric analysis of variance (K); $\delta^{13}C$, $K_4 = 12.39$, $P = 0.006$; $\delta^{15}N$, $K_4 = 12.21$, $P = 0.007$). The Norway rat samples were enriched in both ^{15}N and ^{13}C, indicating significant marine components in their diet (Mean (95% C. I); $\delta^{15}N = 14.35$ (0.6), $\delta^{13}C = -16.03$ (1.48). Fig. 3).
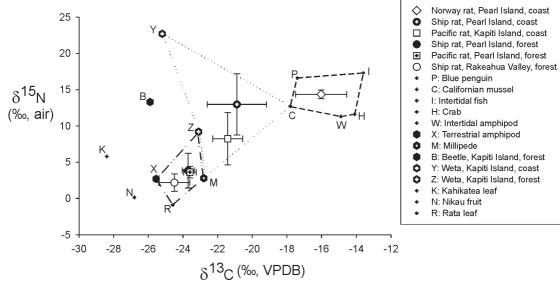

Figure 3. Diet polygons for Norway rats, ship rats and Pacific rats from coastal and forest trap-lines on Pearl, Stewart and Kapiti Islands, in relation to possible marine, intertidal, and terrestrial food sources. Different polygon lines join isotopic values of possible dietary items. Error bars: 95% C.I.

Norway rats were enriched in ^{15}N compared with the mussel and crab species, and slightly more enriched than the blue penguin; they were also enriched in ^{13}C compared with the mussel and blue penguin (Fig. 3). Muscle tissue of the three ship rats trapped on the coastal line was significantly less enriched in ^{13}C than that of the Norway rats trapped at the same site (Mann-Whitney U-test, $U_1 = 0.001$, $P = 0.034$), but there was no significant difference in δ^{15}N values ($U_1 = 8.0$, $P = 0.48$). The ship rats were therefore obtaining more C from the terrestrial food web than were the Norway rats in the same area, but both were obtaining their nitrogen from the same sources.

Ship rats trapped on the forest grids were significantly depleted in ^{15}N compared with the coastal ship rats (δ^{15}N: $U_1 = 12.00$, $P = 0.034$) but not in ^{13}C (δ^{13}C: $U_1 = 9.5$, $P = 0.21$; Fig. 3). There was no significant difference in the δ^{15}N and δ^{13}C values of the ship rats and Pacific rats trapped on the forest grids (δ^{15}N: $U_1 = 4.5$, $P = 0.31$, δ^{13}C: $U_1 = 11.0$, $P = 0.38$). The four Pearl Island forest ship rats were significantly more enriched in ^{13}C than the five ship rats from Stewart Island ($U_1 = 2.00$, $P = 0.048$), but not in ^{15}N ($U_1 = 17.00$, $P = 0.086$). The stable isotopic ratios for ship rats and Pacific rats from the forests of Pearl Island and Stewart Island fell well within the polygons bounded by terrestrial organisms, which suggest these rats were eating a very similar trophic mix of prey.

Discussion

Habitat use

Ship rats were the most common species on Pearl Island and Pacific rats the next most common. This matches results from Stewart Island (Sturmer, 1988, Harper *et al.*, 2005). Unlike on Stewart Island, Pacific rats shared the podocarp-broadleaf forest and shrubland with ship rats on Pearl Island. Other research has suggested that ship rats limit the distribution of Pacific rats (Russell and Clout, 2004), but they were sympatric on Pearl Island. On Stewart Island, predation by cats may restrict the foraging and social interaction of Pacific rats and ship rats more severely than it does for Norway rats (Childs, 1986; Fitzgerald *et al.*, 1991), which in turn may allow Norway rats to share podocarp-broadleaf forest with ship rats, albeit in low numbers (Harper, 2005a). A combination of predation by cats and interference competition from the two larger species may then exclude Pacific rats from this forest type on Stewart Island.

Within the forest the distribution of Pacific and ship rats and overall density of rats varied, with Grid 'L' having an even ratio of species and higher overall population density, but Grid 'K' having substantially more ship rats and a lower overall density. This is unlikely to be due to the different traps used, as rats were trapped to extinction. It is more likely that there were some microhabitat variations within the forest resulting in a patchy distribution of rats (Dowding and Murphy, 1994).

The shrubland appeared to be poor habitat for rats, with a very low trapping rate (Table 1). Trapping at the streams showed similar trapping rates and species ratios as forested grids. As neither Pacific rats nor ship rats are known to forage in fresh water (Atkinson and Towns, 2005; Innes, 2005a), these results probably reflect the similar ratios and species distribution in forest on Pearl Island. The lack of Norway rats trapped in riparian trap-lines, in contrast to results in other sites in New Zealand (Innes, 2005b), suggests either a poor food supply in the streams, and/or competitive exclusion from the surrounding forest by the other species.

Norway rats were trapped only on the coast, in similar numbers to ship rats, and the trapping success was relatively high. This capture rate may reflect a particularly good breeding season rather than an exceptional habitat, as coastal populations of Norway rats elsewhere tend to be in similar numbers as inland populations (Beveridge and Daniel, 1965, Bettesworth and Anderson, 1972). Whether the Norway rats were preferentially selecting the inter-tidal habitat or being prevented from using the forest on Pearl Island is unknown. It is likely that Norway rats were dominating the richest available food, both in terms of energy and protein, on an apparently infertile island. This is probably due to Norway rats' ability to forage in water, which allows them access to food largely unavailable to ship rats (Innes 2005a; 2005b). Although Norway rats were apparently not excluding ship rats from the coast and some marine-derived food, Norway rats appear to be better adapted, physiologically, to this habitat (Harper *et al.* 2005). If Norway rats were being excluded from forest on Pearl Island then the mechanism may have been through more efficient resource use by the smaller species. Smaller species can have advantages in competitive situations, particularly in greater efficiency in energy extraction over most of the size range of foods (Rosenzweig and Sterner, 1970). Larger species should have free access to food due to dominance, and an ability to deal with large or hard food (Grant, 1972). In cases where available food is generally small and/or hard to find, as is often the case with arthropods or plant material like seeds (Gales, 1982; Sturmer, 1988), the Norway rats may be at an energetic disadvantage compared with the two smaller species. For example, during rimu seed-mast events on Stewart Island, only Pacific and ship rat populations subsequently increased (Sturmer, 1988; Harper, 2005a). Despite having similar breeding biology (Atkinson and Towns, 2005; Innes, 2005a, b), Norway rat abundance

did not increase during either event, suggesting a degree of competitive exclusion from this food source. A competitive exclusion hypothesis could be tested by the selective removal of either species from each adjacent habitat and by comparing the available energy and N sources, and species' requirements, in the different habitats.

The differences in food resources on Pearl Island appear to have been linked to habitat. Only on the coast were two species, Norway rats and ship rats, shown to be ingesting different foods within the same habitat. The marine food sources that the Norway rats were utilising were probably of high quality. The isotopic signatures for possible dietary items were significantly more enriched in ^{15}N and ^{13}C than the terrestrial food sources, and hence Norway rats had a primarily marine derived diet. Although gut samples were not obtained to confirm this, the very similar ^{13}C and ^{15}N values relative to blue penguins and an intertidal fish species strongly suggest this. Norway rats are known to forage for freshwater mussels and crayfish (Beveridge and Daniels, 1965; Sturmer, 1988), and on marine foods from the intertidal zone (Bettesworth and Anderson 1972, Moors, 1985; Navarette and Castilla, 1993; Taylor and Thomas, 1993).

The more depleted $\delta^{13}C$ values from ship rats trapped in the same habitat suggested a strong terrestrial component, although the $\delta^{15}N$ values were nearly as enriched as three of the Norway rats and much more enriched than individuals trapped in the forest, so the coastal ship rats were getting most of their protein from the marine food chain. The isotopic values of the ship rats from Pearl Island were similar to those of Pacific rats from Kapiti Island (*n* = 6; Beavan and Sparks, 1998) and their respective dietary polygons (Fig. 3) indicated they were exploiting both marine and terrestrial sources. The possible dietary items shown included a mussel species and a coastal and forest invertebrate species. The wide 95% confidence intervals for the ship rats and Pacific rats trapped in coastal areas resulted from variation in values between individual rats. This suggests some individuals within a population are ingesting more marine-sourced foods than others.

Ship rats and Pacific rats in the forest had virtually identical $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios. This shows that they were deriving all their food from terrestrial sources. Diet was not sampled, so the only known habitat partitioning was a possible temporal delay in reproduction by Pacific rats relative to ship rats. Temporal partitioning in reproduction between competing rodents has been recorded elsewhere (Heske *et al*., 1984). If this is the case then it deserves further investigation.

Density and dispersal

As expected, the low densities of rats recorded on Pearl Island were similar to a density of 2–2.5 rats ha^{-1} recorded on Stewart Island in 1984–1985 (Hickson *et al*., 1986) and were close to densities from the Orongorongo Valley in the North Island in 1966–1969 (Daniel, 1972). Predation by cats occurs at both these sites, but death from chilling in cold wet weather is also likely (Daniel 1972), which would restrain population growth. Similarly, population density in these sites may conceivably be limited by primary productivity. The poor soil fertility on Stewart Island (Wilson, 1987) and poor to medium soil fertility in the Orongorongo Valley (Daniel and Adams, 1984), coupled with the cool and wet climate in both sites, could affect primary productivity (Whitehead *et al*., 2002) and nutrient availability, which in turn inhibit consumer productivity (Cole and Batzli, 1978; Mayntz and Toft, 2001). In warmer mainland sites in the northern North Island, densities of rats ranged from 2.9 rats ha^{-1} to 6.2 rats ha^{-1}, measured mainly earlier in the breeding season than in the current study (Dowding and Murphy, 1994; Hooker and Innes, 1995; Brown *et al*., 1996).

The population densities for Pacific rats on Pearl Island were also low compared with other small islands (Moller and Craig, 1987). On Tiritiri Matangi Island off the northern North Island, for example, Pacific rat densities in small forest patches varied between 6 and 80 ha^{-1}. It is possible that a longer food pulse occurs on Tiritiri Matangi (Moller and Craig, 1987) than on Pearl Island, resulting in more litters per breeding season. The low trapping success indices for most of the Pearl Island sites reflect the low density and were similar to results from forest on Stewart Island (Hickson *et al*., 1986; Sturmer, 1988; Harper *et al.,* 2005). This contrasts with the expected effect of increase in density from reduced predation on islands (Adler and Levins, 1994). Although weka are possible predators, and are known to eat rats on Macquarie Island (Brothers and Skira, 1984), it is unlikely weka significantly affect rat abundance. There appears to be innumerable refuges available on Pearl Island, especially for rats able to climb, and rats are also largely nocturnal. As weka tend to roost at night (Marchant and Higgins, 1993) and their abundance is low, interactions between the species are probably limited. The similar numbers of rats at sites with and without cats also suggests that cat predation is not the major factor limiting rat numbers on Stewart Island.

The limited data from the live-trapping grid suggested that there was no or little dispersal of juvenile ship rats from the higher-density forested portion into the adjacent low-density shrubland. This was unexpected, considering the three-fold difference in densities between the two adjacent grids, and that in this situation the shrubland site should have acted

as a dispersal sink (Gliwicz, 1980), especially as ship rats are present in similar habitat on Stewart Island (Sturmer, 1988; Harper *et al.*, 2005). It is possible that any dispersal was delayed and/or missed by this twelve–day trapping period. The juveniles were large and obviously independent however, so this alternative explanation seems unlikely.

The planned removal of selected rat species did not work in this study, as ship rats and Pacific rats were sharing podocarp-broadleaf forest on Pearl Island, which contrasts with the situation on Stewart Island and adds support to the role of interference from Norway rats (Harper and Veitch *in press*), and possibly predation by cats, in affecting habitat use by Pacific rats. It also adds weight to the suggestion that low ground cover allows Pacific rats to avoid predation (Atkinson and Towns, 2005). This study did show Norway rats and ship rats exploiting different food sources within the coastal habitat. Density and abundance estimates from Pearl Island were low and similar to those on Stewart Island, which implies low ecosystem productivity for the area, and suggests predation by cats is not the main limiting factor for rats on Stewart Island. Although these results strengthen the conclusion that ship rats dominate Norway rats in forest in New Zealand, further temporal and spatial replication is required to clarify the mechanisms discussed. Research would need to test a combination of factors including food amount and quality, habitat structure, and predation risk.

Acknowledgements

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Appendix 1. Stable-nitrogen and -carbon isotope values of lipid-extracted leg muscle tissue for three rat species trapped in two habitat types on Pearl Island and the Rakeahua Valley, Stewart Island, 2004 and 2005. All rats were adults.

Species	Sex	Trap	Date	Habitat	δ^{15}N	δ^{13}C
Pearl Island						
Ship	M	A4L	29 Mar 04	Forest	6.1 (±0.3‰)	-23.4 (±0.3‰)
Ship	F	A4L	27 Mar 04	Forest	3.0	-23.8
Ship	M	D1L	27 Mar 04	Forest	3.1	-23.9
Ship	M	HCRK	5 Apr 04	Forest	3.2	-23.7
Pacific	M	D5L	26 Mar 04	Forest	3.3	-23.3
Pacific	F	D5L	28 Mar 04	Forest	3.2	-23.5
Pacific	F	A2L	28 Mar 04	Forest	4.3	-23.7
Pacific	M	F4L	31 Mar 04	Forest	3.7	-23.8
Norway	F	52	15 Jun 05	Coast	14.6	-15.1
Norway	F	50	15 Jun 05	Coast	14.4	-17.3
Norway	F	38	15 Jun 05	Coast	14.6	-15.7
Norway	F	51	15 Jun 05	Coast	13.8	-16.0
Ship	M	58	16 Jun 05	Coast	12.3	-21.1
Ship	F	17	15 Jun 05	Coast	11.7	-20.1
Ship	F	56	15 Jun 05	Coast	14.9	-21.4
Rakeahua Valley						
Ship	F	S16	19 Jun 05	Forest	2.0	-25.4
Ship	F	S21	19 Jun 05	Forest	2.5	-25.1
Ship	M	S05	19 Jun 05	Forest	3.7	-23.8
Ship	F	N07	18 Jun 05	Forest	1.2	-23.9
Ship	F	S07	19 Jun 05	Forest	1.6	-24.3